Grooming and group cohesion in primates: implications for the evolution of language

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Abstract: It is well established that allogrooming, which evolved for a hygienic function, has acquired an important derived social function in many primates. In particular, it has been postulated that grooming may play an essential role in group cohesion and that human language, as verbal grooming or gossip, evolved to maintain group cohesion in the hominin lineage with its unusually large group sizes. Here, we examine this group cohesion hypothesis and test it against the alternative grooming-need hypothesis which posits that rates of grooming are higher in species where grooming need (i.e. the motivation to groom for hygiene and its associated psychological reward) is more pronounced. This alternative predicts that the derived social function of grooming evolved mostly in those lineages that had the highest exposure to ectoparasites and dirt, i.e. terrestrial species. A detailed comparative analysis of 74 species of wild primates, controlling for phylogenetic non-independence, showed that terrestriality was a highly significant predictor of allogrooming time, consistent with the prediction. The predictions of the group cohesion hypothesis were not supported, however. Group size did not predict grooming time across primates, nor did it do so in separate intra-population analyses in 17 species. Thus, there is no comparative support for the group-cohesion function of allogrooming, which questions the role of grooming in the evolution of human language.

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Supplementary Information

Table S1: Grooming and group size in primates. Whenever data on individual groups were given in the primary literature, we used group as a single entry in the table. In some cases, however, only averaged data for the whole population comprising two or more groups were available.

Species	Site	n (grps)	Group size (community/ band size in brackets)	Grooming (%)	Source	Comments
Avahi laniger	Ranomafana	1	2	2	C. Harcourt in (1)	
Lemur catta	Antserananomby	1	19	4.67	(2)	Mutual and self-grooming may have been put together in the category "grooming." Data mainly from the intensively observed AC1; BC1-BC2 excluded from mean group size
Lemur catta	Berenty	2	17.5	11	(2)	Behavioral data recorded only for troops adjacent to the river (p.40) i.e. B-F (Fig. 3)
Eulemur fulvus	Antserananomby	12	9.2	5.25	(2)	Mutual and self-grooming may have been put together in the category "grooming"
Eulemur fulvus	Tongobato	5	10.2	11.3	(2)	Mutual and self-grooming may have been put together in the category "grooming." Only 3 groups studied, but not mentioned which ones. Mean group size of TF1-TF5 used.
Propithecus verreauxi	Kirindy	5	5.6	2	(3)	
Saguinus mystax	Quebrada Blanco	1	4	1.85	(4)	
Cebus olivaceus	Hato Masaguaral	1	8	1.5	(5)	
Cebus olivaceus	Hato Masaguaral	1	25	2.2	(5)	
Cebus apella	Manu	1	16	0.91	van Schaik, unpubl.	
Cebus apella	Manu	1	13.2	1.5	(6)	Grooming

						included in miscellaneous ~ 1,5% (Fig. 4.1) and "most of the total is comprised of allogrooming bouts" (p. 51)
Cebus albifrons	Manu	1	8.5	0	(6)	Grooming included in "miscellaneous = 0%" (Fig. 4.1)
Cebus albifrons	Manu	2	13	1.23	van Schaik, unpubl.	
Callicebus oenanthe	Rio Mayo	1	4	4.5	(7)	
Callicebus torquatus	Estación Biológica Callicebus	1	4	9.9	(8)	
Chiropotes satanas	Tucuruí	1	32	0.4	(9)	Group size given as range across study period; we took midpoint; group Su not included since visibility was low
Pithecia pithecia	Estado Bolivar	1	8	0.8	(10)	
Cacajao calvus	Lago Preto	NA	44	1.8	(11)	
Alouatta palliata	Barro Collorado	1	13	0	(12)	Grooming included in "interaction", but "no allo-grooming occurs" (p. 253)
Alouatta seniculus	Finca Merenberg	1	9.5	0.4	(13)	
Alouatta guariba	El Piñalito	1	7.5	2.1	Agostini, unpubl., (14)	
Alouatta guariba	El Piñalito	1	4	4.1	Agostini, unpubl., (14)	
Alouatta guariba	Santa Genebra	1	6	2	(15)	
Alouatta caraya	El Piñalito	1	13	1.9	Agostini, unpubl., (14)	
Alouatta caraya	El Piñalito	1	6	0.4	Agostini, unpubl., (14)	
Ateles geoffroyi	Barro Collorado	1	UNK (15)	2.5	(16)	
Ateles belzebuth	Yasuni	1	UNK (16)	0.1	(17)	0.1 = time spent in social behavior
Brachyteles hypoxanthus	Fazenda Montes Claros	1	UNK (34)	0	(18)	
Presbyis siamensis	Kuala Lompat	1	18	0	(19)	
Presbytis thomasi		6	5.8	1.3	(20)	
Presbytis potenziani	Muntei	1	6	0.1	(21)	% grooming <0.1
Presbytis rubicunda	Sepilok	1	7	0	(22)	

Trachypithecus leucocephalus	Fusui	2	10.5	11.5	(23, 24)	
Trachypithecus pileatus	Madhupur	1	13	0.35	(25)	
Trachypithecus francoisi	Nonggang	1	12	2	(26)	
Trachypithecus francoisi	Mayanghe	1	7	0.33	(27)	
Semnopithecus achates	Jodhpur	1	12	6	(28)	Females only
Semnopithecus entellus	Kanha	1	20	6	(29)	
Semnopithecus cf. *schistaceus*	Machiara	1	71	8.45	(30)	
Semnopithecus cf. *schistaceus*	Machiara	1	184	14.17	(30)	
Semnopithecus schistaceus	Simla	1	34	4.4	(31)	TK troop
Semnopithecus schistaceus	Langtang	1	30	9.5	(32)	
Rhinopithecus bieti	Wuyapiya	1	11.5 (175)	6.1	(33)	
Rhinopithecus bieti	Samage	1	NA (410)	7.3	(34)	
Rhinopithecus avunculus	Na Hang	5	15.2	6.8	(35)	One-male unit size
Rhinopithecus avunculus	Khau Ca	5	11.3	4.3	(36, 37)	One-male unit size
Pygtahrix nigripes	Nui Chua & Phuoc Binh	NA	11.6	2.25	(38)	Mean of mean group sizes at 2 sites
Pygathrix nemaeus	Hin Namno, Laos	2	28	1.78	(39)	
Nasalis larvatus	Sukau	1	20	2.8	(40)	
Colobus polykomos	Tiwai	UNK	9	0.7	G. Dasilva (1)	
Colobus guereza	Kakamega	1	11	5.6	(41)	
Colobus guereza	Kakamega	1	7	6.7	(41)	
Colobus guereza	Kanyawara	1	9	6.2	(42)	
Colobus satanas	Douale-Edea	1	16	5.5	(43)	Includes self-cleaning
Colobus angolensis	Nyungwe	1	300	5	(44)	Group size >300
Colobus vellerosus	Boabeng-Fiema	1	32	2.34	(45)	
Colobus vellerosus	Boabeng-Fiema	1	7.5	0.38	(45)	
Colobus vellerosus	Boabeng-Fiema	1	15.5	0.35	(45)	
Piliocolobus rufomitratus	Tana River	1	19	2.1	(46)	
Piliocolobus temminckii	Abuko	1	27	5.4	(47)	
Piliocolobus	Jozani	1	23	6.24	(48)	TTK forest group

kirkii						
Piliocolobus kirkii	Jozani	1	36	5.14	(48)	Miwaleni forest group
Piliocolobus kirkii	Jozani	1	34	4.7	(48)	Kwa Joshi forest group
Piliocolobus kirkii	Jozani	1	20	7.39	(48)	Shamba group 1
Piliocolobus kirkii	Jozani	1	65	9.48	(48)	Shamba group 3
Piliocolobus kirkii	Jozani	1	38	8.59	(48)	Shamba group 4
Piliocolobus kirkii	Jozani	1	26	7.7	(48)	Shamba group 5
Piliocolobus tephrosceles	Gombe	1	82	5.8	(49)	
Piliocolobus tephrosceles	Kibale	1	19.9	4.5	(50)	
Procolobus verus	Tai	UNK	3	3.6	R. Noe & A. H. Korstjens in (51)	
Cercopithecus mitis	Cape Vidal	1	32	8	(52)	Incl. self-grooming
Cercopithecus mitis	Kibale	1	25	9.1	(53)	At beginning of study (1973-74); adult females only
Cercopithecus mitis	Kibale	1	12	9.4	(53)	Adult females only
Cercopithecus mitis	Kibale	1	27	6.3	(53)	Adult females only
Cercopithecus mitis	Kibale	1	27	8.5	(53)	Adult females only
Cercopithecus mitis	Kibale	1	18	7	(53)	At end of study (1978-80); adult females only
Cercopithecus ascanius	Kibale	1	32.5	5.6	(50)	
Cercopithecus campbelli	Tai	1	9	2.8	(54)	
Cercopithecus diana	Tai	1	28.8	2.5	(54)	
Chlorocebus aethiops	Amboseli	2	15	8.6	(55)	Group sizes estimated from Fig1
Chlorocebus aethiops	Amboseli	4	9.8	5	(55)	Group sizes estimated from Fig. 1
Chlorocebus djamdjamensis	Odobullu, Ethiopia	2	53	2.7	(56)	
Lophocebus albigena	Kibale	1	13.5	4	(57)	Mean group size across study; female-female grooming only
Lophocebus albigena	Kibale	1	13	7	(57)	Mean group size across study; female-female grooming only
Lophocebus albigena	Kibale	1	14	4	(57)	Mean group size across study;

						female-female grooming only
Lophocebus albigena	Kibale	1	15.5	6	(57)	Mean group size across study; female-female grooming only
Lophocebus albigena	Kibale	1	19	5	(57)	Mean group size across study; female-female grooming only
Cercocebus galeritus	Tana	?	27	5.5	(58)	
Erythrocebus patas	Kala Maloue	1	16	1	(59)	
Erythrocebus patas	Mutara	1	20	9.5	(60)	Females only
Erythrocebus patas	Mutara	1	50	3.1	(60)	Females only
Macaca fascicularis	Ketambe	4	29.3	10.6	van Noordwijk, unpubl.	
Macaca fuscata	Yakushima	1	12	18.9	(61)	Group size given as range across study period; we took midpoint
Macaca fuscata	Yakushima	1	47	27.9	(62)	
Macaca fuscata	Shiga Heights	1	24	7.2	(63)	
Macaca mulatta	Kathmandu	1	84	6.6	(64)	
Macaca munzala	Zemithang	2	18	12	(65)	
Theropithecus gelada	Sankaberj	3	13 (144.7)	17.4	(66, 67)	Datum on grooming taken from Lehmann et al. (2007); datum on unit size is the mean of unit sizes from Bole, Sankaber, and Gich
Papio anubis	Awash	1	71	9.1	(68)	
Papio anubis	Gilgil	1	36	5.6	(69)	
Papio anubis	Gilgil	1	57	4.6	(69)	
Papio papio	Mt. Assirik	2	192.5	8.3	(70)	
Papio hamadryas	Awash	1	7.5 (51)	13.5	(68, 71)	
Papio ursinus	Drakensberg	1	18	8	(72)	
Papio ursinus	Drakensberg	1	36	12	(72)	
Papio ursinus	De Hoop	1	19	14	(72)	
Papio ursinus	De Hoop	1	44	17	(72)	
Hylobates lar	Kao Yai	1	5	6	(73)	
Hylobates lar	Kao Yai	1	6	7.2	(73)	
Hylobates lar	Kuala lompat	1	4	3	(74)	
Hylobates lar	Malayan Peninsula	4	3.25	1.4	(75)	Group size based on 28 groups

Hylobates klossii	Paitan		3.8	0	(76)	
Hylobates agilis	Sungai Dal		4	0	(74)	
Hylobates pileatus	Khao Soi Dao	1	6	5	(77)	
Symphalangus syndactylus	Ulu Sempam	1	4	12	(78)	
Symphalangus syndactylus	Kuala Lompat	1	5	15	(78)	Same siamang group
Symphalangus syndactylus	Kuala Lompat	1	4	1	(74)	Same siamang group
Pan paniscus	Lomako	UNK	6.2 (27.8)	5.7	(79, 80)	Community size taken from Lehmann et al. (2007)
Pan troglodytes	Gombe	2	UNK (28)	6.2	(81)	
Pan troglodytes	Tai	1	10 (60)	9	(82)	
Pan troglodytes	Mahale	1	UNK (100)	14.1	(83)	Data from 1985
Gorilla gorilla	Mondika	UNK	11	0.09	Doran, cited in (51)	
Gorilla beringei	Karisoke	1	47	3.22	Karisoke, long term records (2008)	
Gorilla beringei	Karisoke	1	12	0.02	Karisoke, long term records (2008)	
Gorilla beringei	Karisoke	1	7	3.54	Karisoke, long term records (2008)	
Gorilla beringei	Karisoke	1	5	2.32	Karisoke, long term records (2008)	
Gorilla beringei	Karisoke	1	29	2.29	Karisoke, long term records (2008)	
Gorilla beringei	Karisoke	1	9	2.65	Karisoke, long term records (2008)	
Gorilla beringei	Karisoke	1	14	3.38	Karisoke, long term records (2008)	
Pongo pygmaeus	Borneo	UNK	1.2	0.01	(84)	Means of populations
Pongo abelii	Sumatra	UNK	1.8	0.01	(84)	Means of populations

1. Dunbar RIM (1991) Functional significance of social grooming in primates. *Folia Primatol* 57:121-131.
2. Sussman RW (1977) In *Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes*, ed Clutton-Brock TH (Academic Press, New York), pp 1-36.
3. Lewis RJ (2010) Grooming patterns in Verreaux's sifaka. *Am J Primatol* 72:254-261.
4. Heymann EW (1996). Social behavior of wild moustached tamarins, *Saguinus mystax*, at the Estacion Biologica Quebrada Blanco, Peruvian Amazonia. *Am J Primatol* 38:101-113.
5. de Ruiter JR (1986) The influence of group size on predator scanning and foraging behaviour of wedgecapped capuchin monkeys (*Cebus olivaceus*). *Behaviour* 98:240-258.
6. Terborgh J (1983) *Five New World Primates: A Study in Comparative Ecology* (Princeton University Press, Princeton).
7. DeLuycker A (2007) *The Ecology and Behavior of the Río Mayo Titi Monkey (*Callicebus oenanthe*) in the Alto Mayo, northern Peru*, Ph.D. thesis (Washington University, St. Louis).
8. Kinzey WG, Wright PC (1982) Grooming behavior in the titi monkey (*Callicebus torquatus*). *Am J Primatol* 3:267-275.
9. Silva SSB, Ferrari SF (2009). Behavior patterns of southern bearded sakis (*Chiropotes satanas*) in the fragmented landscape of eastern Brazilian Amazonia. *Am J Primatol* 71:1-2.
10. Homburg I (1998) *Oekologie und Sozialverhalten von Weissgesicht-Sakis*, Ph.D. thesis (Universität Bielefeld, Bielefeld, Germany).
11. Bowler M, Bodmer R (2009). Social behaviour in fission-fusion groups of red uakari monkeys (*Cacajao calvus ucayalii*). *Am J Primatol* 71: 976-987.
12. Richard A (1970). A comparative study of the activity patterns and behavior of *Alouatta villosa* and *Ateles geoffroyi*. *Folia Primatol* 12:241-263.
13. Gaulin SJC, Gaulin CK (1982) Behavioral ecology of *Alouatta seniculus* in Andean cloud forest. *Int J Primatol* 3:1-32.
14. Agostini I, Holzmann I, Di Bitetti MS (2010). Are howler monkey species ecologically equivalent? Trophic niche overlap in syntopic *Alouatta guariba clamitans* and *Alouatta caraya*. *Am J Primatol* 72:173-186.
15. Chiarello AG (1995). Grooming in brown howler monkeys, *Alouatta fusca*. *Am J Primatol* 35:73-81.
16. Ahumada JA (1992) Grooming behavior of spider monkeys (*Ateles geoffroyi*) on Barro Colorado Island, Panama. *Int J Primatol* 13:33-49.
17. Suarez SA (2006) Diet and travel costs for spider monkeys in a nonseasonal, hyperdiverse environment. *Int J Primatol* 27:411-436.
18. Strier KB (1992). *Faces in the Forest: The Endangered Muriqui Monkeys of Brazil* (Oxford University Press, Oxford).
19. Bennett E (1983) *The Banded Langur: Ecology of a Colobine in West Malaysian Rain-Forest*, Ph.D. thesis (Sidney Sussex College, Cambridge).
20. van Oijen JAMC (1992) *Sex Differences in Feeding Behaviour of Adult Thomas Langurs*, Doctoral thesis (Utrecht).
21. Sangchantr S (2004) *Social Organization and Ecology of Mentawai Leaf Monkeys (*Presbytis potenziani*)*, Ph.D. thesis (Columbia University, New York).
22. Davies AG (1984) *An Ecological Study of the Red Leaf Monkey (*Presbytis rubicunda*) in the Dipterocarp Forest of Northern Borneo*, Ph.D. thesis (University of Cambridge, Cambridge).
23. Li Z, Rogers ME (2004a). Social organization of white-headed langurs *Trachypithecus leucocephalus* in Fusui, China. *Folia Primatol* 75:97-100.
24. Li Z, Rogers ME (2004b). Habitat quality and activity budgets of white-headed langurs in Fusui, China. *Int J Primatol* 25:41-54.
25. Stanford CB (1991). *The Capped Langur in Bangladesh: Behavioral Ecology and Reproductive Tact*ics (Karger, Basel).
26. Zhou QH, Wei FW, Huang CM, Li M, Ren BP, Luo B (2007) Seasonal variation in the activity patterns and time budgets of *Trachypithecus francoisi* in the Nonggang Nature Reserve, China. *Int J Primatol* 28:657-671.
27. Luo Y, Zhang M, Ma J, Wu A, Wang S, Zhang S (2007) Time budget of daily activity of Francois' langur (*Trachypithecus francoisi francoisi*) in disturbance habitat. *Acta Ecol Sin* 27:1715-1722.

28. Borries C, Sommer V, Srivastava A (1994). Weaving a tight social net: allogrooming in free-ranging female langurs (*Presbytis entellus*). *Int J Primatol* 15:421-443.
29. Newton P (1992) Feeding and ranging patterns of forest hanuman langurs (*Presbytis entellus*). *Int J Primatol* 13:245-285.
30. Minhas RA, Ahmed KB, Awan MS, Dar NI (2010) Social organization and reproductive biology of Himalayan grey langur (*Semnopithecus entellus ajex*) in Machiara National Park, Azad Kashmir (Pakistan). *Pakistan J Zool* 42:143-156.
31. Sugiyama Y (1976) Characteristics of the ecology of the Himalayan langurs. *J Hum Evol* 5:249-277.
32. Sayers K, Norconk MA (2008) Himalayan *Semnopithecus entellus* at Langtang National Park, Nepal: diet, activity patterns, and resources. *Int J Primatol* 29:509-530.
33. Kirkpatrick RC (1996) *Ecology and Behavior of the Yunnan Snub-Nosed Langur (*Rhinopithecus bieti*, Colobinae)*, Ph.D. thesis (University of California, Davis).
34. Grueter CC (2009) *Determinants of Modular Societies in Snub-Nosed Monkeys (*Rhinopithecus bieti*) and Other Asian Colobines*, Ph.D. thesis (University of Zurich, Zurich, Switzerland).
35. Boonratana R, Le XC (1998) In *The Natural History of the Doucs and Snub-nosed Monkeys*, ed Jablosnki NG (World Scientific, Singapore), pp 207-215.
36. Dong TH (2007) *Behavioural Ecology and Conservation of* Rhinopithecus avunculus *in Vietnam*, MSc thesis (Australian National University, Canberra).
37. Dong TH (2010) Social organization and range use size in Tonkin snub-nosed monkeys (*Rhinopithecus avunculus*) in Khau Species and Habitat Conservation Area. *Primate Res* 26 (Suppl.):Abstract #660.
38. Hoang MD (2007) *Ecology and Conservation Status of the Black-Shanked Douc (*Pygathrix nigripes*) in Nui Cha and Phuoc Binh National Parks, Ninh Thuan Province, Vietnam*, Ph.D. thesis (University of Queensland, Brisbane).
39. Phiapalath P, Suwanwaree P (2010) In *Conservation of Primates in Indochina*, eds Nadler T, Rawson BM, Van NT (Frankfurt Zoological Society and Conservation International, Hanoi).
40. Boonratana R (1993) *The Ecology and Behaviour of the Proboscis Monkey (*Nasalis larvatus*) in the Lower Kinabatangan*, Ph.D. thesis (Mahidol University, Sabah).
41. Fashing PJ (2001) Activity and ranging patterns of guerezas in the Kakamega Forest: Intergroup variation and implications for intragroup feeding competition. *Int J Primatology* 22:549-577.
42. Oates JF (1977) In *Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes*, ed Clutton-Brock TH (Academic Press, New York), pp 275-321.
43. McKey D, Waterman PG. (1982) Ranging behaviour of a group of black colobus (*Colobus satanas*) in the Douala-Edea Reserve, Cameroon. *Folia Primatol* 39:264-304.
44. Fashing PJ et al. (2007) Activity and Ranging patterns of *Colobus angolensis ruwenzorii* in Nyungwe Forest, Rwanda: possible costs of large group size. *Int J Primatol* 28:529-550.
45. Teichroeb JA, Saj TL, Paterson JD, Sicotte P (2003) Effect of group size on activity budgets of *Colobus vellerosus* in Ghana. *Int J Primato*l 24:743-758.
46. Marsh CW (1981) Time budget of Tana River red colobus. *Folia Primatol* 35:30-50.
47. Starin ED (1991) *Socioecology of the Red Colobus Monkey in the Gambia with Particular Reference to Female-Male Differences and Transfer Patterns*, Ph.D. thesis (City University of New York, New York).
48. Siex KS (2003) *Effects of Population Compression on the Demography, Ecology, and Behavior of the Zanzibar Red Colobus Monkey (*Procolobus kirkii*),* Ph.D. thesis (Duke University, Durham).
49. Clutton-Brock TH (1974) Activity patterns of red colobus (*Colobus badius tephrosceles*). *Folia Primatol* 21:161-187.
50. Struhsaker TT, Leland L (1979). Socioecology of five sympatric monkey species in the Kibale Forest, Uganda. *Adv Stud Behav* 9:159-228.
51. Lehmann J, Korstjens AH, Dunbar RIM (2007) Group size, grooming and social cohesion in primates. *Anim Behav* 74:1617-1629.
52. Lawes MJ, Piper SE (1992) Activity patterns in free-ranging samango monkeys (*Cercopithecus mitis erythrarchus* Peters, 1852) at the southern range limit. *Folia Primatol* 59:186-202.
53. Butynski TM (1990). Comparative ecology of blue monkeys (*Cercopithecus mitis*) in high- and low-density subpopulations. *Ecol Monogr* 60:1-26.

54. Buzzard PJ (2004) *Interspecific competition among* Cercopithecus campbelli*,* Cercopithecus petaurista*, and* Cercopithecus diana *at Tai Forest, Cote d'Ivoire (Cote d'Ivoire)*, PhD thesis (Columbia University, New York).
55. Isbell LA, Young TP (1993) Social and ecological influences on activity budgets of vervet monkeys, and their implications for group living. *Behav Ecol Sociobiol* 32:377-385.
56. Mekonnen A, Bekele A, Fashing PJ, Hemson G, Atickem A. (2010) Diet, activity patterns, and ranging ecology of the Bale monkey (*Chlorocebus djamdjamensis*) in Odobullu Forest, Ethiopia. *Int J Primatol* 31:339-362.
57. Chancellor R, Isbell L (2009) Female grooming markets in a population of gray-cheeked mangabeys (*Lophocebus albigena*). *Behav Ecol* 20:79-86.
58. Homewood KM (1976) *Ecology and Behaviour of the Tana Mangabey,* Cercocebus galeritus galeritus, Ph.D. thesis (University of London, London).
59. Nakagawa N (1989) Activity budget and diet of patas monkeys in Kala Maloue National Park, Cameroon: a preliminary report. *Primates* 30:27-34.
60. Chism J, Rogers W (2002) In *The Guenons: Diversity and Adaptation in African Monkeys*, eds Glenn ME, Cords M (Kluwer, New York), pp 233-244.
61. Agetsuma N (1995). Foraging strategies of Yakushima macaques (*Macaca fuscata yakui*). *Int J Primatol* 16:595-609.
62. Maruhashi T (1981) Activity patterns of a troop of Japanese monkeys (*Macaca fuscata yakui*) on Yakushima Island, Japan. Primates 22:1-14.
63. Wada K, Tokida E (1981) Habitat utilization by wintering Japanese monkeys (*Macaca fuscata fuscata*) in the Shiga Heights. *Primates* 22:330-348.
64. Marriott BM (1988) In *Ecology and Behavior of Food-enhanced Primate Groups*, ed Fa JE, Southwick CH (Alan R. Liss, New York), pp 125-149.
65. Kumar RS, Mishra C, Sinha A (2007) Foraging ecology and time-activity budget of the Arunachal macaque *Macaca munzala*: a preliminary study. *Curr Sci* 93:532-539.
66. Dunbar RIM (1984) *Reproductive Decisions: An Economic Analysis of Gelada Baboon Social Strategies*. Princeton University Press, Princeton.
67. Iwamoto T, Dunbar RIM (1983) Thermoregulation, habitat quality and the behavioural ecology of gelada baboons. *J Anim Ecol* 52:357-366.
68. Nagel U (1973) A comparison of anubis baboons, hamadryas baboons and their hybrids at a species border in Ethiopia. *Folia Primatol* 19:104-165.
69. Eley RM, Strum SC, Muchemi G, Reid GDF (1989) Nutrition, body condition, activity patterns, and parasitism of free-ranging troops of olive baboons (*Papio anubis*) in Kenya. *Am J Primatol* 18:209-219.
70. Sharman M (1981) *Feeding, Ranging and Social Organization of the Guinea Baboon*, Ph. D. thesis (University of St. Andrews, St. Andrews).
71. Stammbach E (1987) In *Primate Societies*, eds Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (University of Chicago Press, Chicago), pp 112-120.
72. Barrett L, Henzi SP, Weingrill T, Lycett JE, Hill RA (1999) Market forces predict grooming reciprocity in female baboons. *Proc Biol Sci* 266:665-670.
73. Bartlett TQ (1999) *Feeding and Ranging Behavior of the White-handed Gibbon (*Hylobates lar*) in Khao Yai National Park, Thailand*, Ph.D. thesis (Washingon University, St. Louis).
74. Gittins SP, Raemaekers JJ (1980). In *Malayan Forest Primates: Ten Years' Study in Tropical Rain Forest* (Plenum, New York), pp 63-105.
75. Ellefson JO (1974) A natural history of white-handed gibbons in the Malayan peninsula. *Gibbon and siamang* 3:1-136.
77. Srikosamatara S (1984) In *The Lesser Apes: Evolutionary and Behavioural Biology*, eds Preuschoft H , Chivers DJ, Brockelman WY, Creel N (Edinburgh University Press, Edinburgh), pp 242-257.
76. Whitten, A. 1980. *The Kloss Gibbon in Siberut Rain Forest*. Ph.D. thesis, University of Cambridge.
78. Chivers DJ (1974) *The Siamang in Malaya: A Field Study of a Primate in Tropical Rain Forest* (Karger, Basel).
79. White FJ (1988) Party composition and dynamics in *Pan paniscus*. *Int J Primatol* 9:179-193.
80. White FJ (1992). Activity budgets, feeding behavior, and habitat use of pygmy chimpanzees at Lomako, Zaire. *Am J Primatol* 26:215-223.

81. Wrangham RW (1977) In *Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes*, ed Clutton-Brock TH (Academic Press, New York), pp 503-538.
82. Boesch C, Boesch-Achermann H. (2000). *The Chimpanzees of the Tai forest: Behavioural Ecology and Evolution* (Oxford University Press, New York).
83. Huffman MA (1990) In *The Chimpanzees of the Mahale Mountains: Sexual and Life History Strategies*, ed Nishida T (University of Tokyo Press, Tokyo), pp 237-255.
84. Wich SA, Utami Atmoko SS, Mitra Setia T, van Schaik CP (2009) *Orangutans: Geographic Variation in Behavioral Ecology and Conservation* (Oxford University Press, New York).

Supplementary Information

Table S2: Phylogenetic general least-squares model with grooming as the response variable, and terrestriality, body mass and group size and interactions between them as possible effects, using *unit* or *party size* as a measure of group size; *including interactions*.

	Primates		**Catarrhini**		**Cercopithecoidea**		**Platyrrhini**	
N	71		54		43		16	
r^2 adjusted	0.210		0.195		0.239		0.277	
AICc	445.0		345.4		265.8		99.9	
lambda: ML-estimate	0.587		0.717		0.806		0	
p of lambda >0	0.106		1		0.017		1	
p of lambda <1	<0.0001		<0.0001		<0.0001		0.0003	
	p	*effect*	*p*	*effect*	*P*	*effect*	*P*	*effect*
ln female body mass	0.055	-3.63	0.390	-2.73	0.813	-1.59	0.951	-0.29
terrestriality	0.005	12.93	0.005	13.7	0.009	15.1	all arboreal	
ln group size	0.246	-8.81	0.567	-6.35	0.558	-11.7	0.797	4.3
ln group size*terrestriality	0.124	-2.31	0.100	-2.65	0.075	-3.36		
ln group size*ln female body mass	0.277	0.88	0.616	0.59	0.609	1.10	0.692	-0.84

Supplementary Information

Table S3: Phylogenetic general least-squares model with grooming rate as the response variable, and terrestriality, body mass and group size and interactions between them as possible effects, using *band size* as a measure of group size**;** a) *including interactions*, b) *excluding interactions*.

a)

	Primates		**Catarrhini**		**Cercopithecoidea**		**Platyrrhini**	
N	74		54		43		16	
r^2 adjusted	0.260		0.394		0.229		0.277	
AICc	460.7		341.5		267.2		99.9	
lambda: ML-estimate	0.458		0		0.755		0	
p of lambda >0	0.055		1		0.110		1	
p of lambda <1	<0.0001		<0.0001		<0.0001		0.0003	
	p	*effect*	*p*	*effect*	*p*	*effect*	*p*	*effect*
ln female body mass	0.014	-4.23	0.153	-3.58	0.595	-3.72	0.951	-0.29
terrestriality	0.186	5.98	0.222	5.95	0.048	11.6	all arboreal	
ln group size	0.246	-7.66	0.760	-2.58	0.496	-13.6	0.797	4.3
ln group size*terrestriality	0.937	0.11	0.998	-0.003	0.240	-2.07		
ln group size*ln female body mass	0.159	0.99	0.582	0.499	0.495	1.49	0.692	-0.84

b)

	Primates		**Catarrhini**		**Cercopithecoidea**		**Platyrrhini**	
N	74		54		43		16	
r^2 adjusted	0.273		0.414		0.246		0.323	
AICc	456.1		334.7		261.2		95.2	
lambda: ML-estimate	0.384		0		0.732		0	
p of lambda=0	0.115		1		0.176		1	
p of lambda=1	<0.0001		<0.0001		<0.0001		0.0001	
	p	*effect*	*p*	*effect*	*p*	*effect*	*p*	*effect*
ln female body mass	0.015	-2.28	0.032	-2.35	0.835	0.47	0.213	-2.03
terrestriality	<0.0001	6.68	0.001	6.22	0.007	5.28	all arboreal	
ln band size	0.045	1.27	0.005	1.99	0.242	0.86	0.189	-2.28